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Associational resistance and shared doom: effects of epibiosis on herbivory

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Abstract The potential for spatial associations between palatable and unpalatable plant species to reduce herbivore pressure on the palatable species has been described as associational resistance, associational refuge or associational defense for numerous terrestrial and marine communities. One of the closest associations between species – epibiosis – has not been thoroughly investigated in this regard. In this study we evaluated how different associations between host seaweeds and epibiotic plants and animals influenced the movement of an omnivorous sea urchin (*Arbacia punctulata*) to the host and subsequent feeding on the host. *A. punctulata* showed clear preferences when given pairwise choices between 12 prey species (3 animals, 9 algae). These preferences were consistent and allowed us to rank the six epibiont species and six host species linearly from least to most preferred by *A. punculata*. Most host-epibiont associations dramatically changed urchin preference, increasing or decreasing urchin grazing on fouled hosts as compared to clean conspecifics. Herbivory on the host increased when the epibiont was more preferred, and decreased when it was less preferred than the unfouled host alga. Taking the host species as a point of reference, we classified epibiosis-caused decrease in herbivory as associational resistance, while epibiont-caused increases in herbivory were defined as shared doom. These epibiont-host-herbivore interactions could select for hosts that facilitate the growth of certain low preference epibionts on their surfaces in situations where the resulting decreases in herbivory would offset the various negative effects of being fouled. In contrast, in situations where herbivores are common, the negative effects of being fouled by palatable epibionts may be much greater than is generally assumed. In our assays, unpalatable hosts fouled by palatable epibionts became much more attractive to urchins and rose several ranks on the urchins' preference hierarchy.

Key words Fouling · Epibiosis · Host-epibiont-herbivore interactions · Plant-herbivore interactions

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Introduction

Susceptibility of a plant to herbivory is seldom related only to its food quality and defenses. Rather, since the 1970s for terrestrial environments and the 1980s for marine environments, community aspects have been shown to strongly influence a species' risk of herbivore attack. Tahvanainen and Root (1972) and Root (1973) introduced the notion of associational resistance, although they did not use this term. This concept was further developed for the terrestrial environment (Atsatt and O'Dowd 1976; McNaughton 1978; Bach 1980) and adapted for marine communities (Hay 1986; Littler et al. 1986; Pfister and Hay 1988). The idea is that a species' susceptibility to consumers is not determined by its deterrent characteristics or food quality per se, but by these properties relative to the characteristics of other members of the community. Thus, a preferred species may be less at risk when surrounded by more preferred species than when growing alone, or it may gain protection by growing close to a repellent, or unpalatable, species. In the first case, herbivores are distracted from the species under consideration due to its more attractive neighbors (attractant/decoy scenario); in the second case, the plant is not discovered because its cues are diluted or masked by those of its repellent neighbors (repellent plant scenario of Atsatt and O'Dowd 1976). On a slightly different line, Martin (1988) found that foraging efficiency of bird egg predators decreases with increasing diversity of nest sites (mixed population), as compared to equally abundant but similar nest sites (one-species population). The effective distance between associates in these rela-

tionships is determined by the foraging behavior and discriminative capabilities of the herbivores (Morris and Karieva 1991). Consequently, attractiveness is not an absolute property of a plant species but may vary with changes in neighboring components of the community as well as with seasons, nutritional conditions, physiological stages, stress, herbivore damage, etc. (see Denno and McClure 1983; Renaud et al. 1990; Cronin and Hay, to be published).

The closest spatial association between different species, short of endoparasitism, is epibiosis. Consequences of epibiosis unrelated to effects on consumers have been studied extensively in marine systems (reviewed in Davis et al. 1989; Wahl 1989; William and Seed 1992). These studies most often focus on negative effects on the host in terms of decreased light and nutrient availability, a loss of flexibility resulting in increased brittleness, changes of surface pH, mechanical damage of host surfaces, and changes in drag, which can cause breakage during storms. In contrast to the numerous studies of fouling's direct negative effects on hosts, studies of how fouling may indirectly affect the host by altering its susceptibility to herbivores are rare.

One benefit of certain epibiotic associations could be a protection of the host from predation through optical or chemical camouflage or through epibiont production of defenses. Only a few studies mention epibiosis effects that can be interpreted as associational resistance (Hay 1986; Feifarek 1987; Barkai and McQuaid 1988; Gil-Turnes et al. 1989).

Curiously, all existing studies on associational resistance only consider the benefits of a palatable species experiencing reduced losses to herbivory when associated with other species. As protection in these cases is never complete, it is reasonable to expect that the less palatable partner in such an association may encounter an increase in herbivory caused by the presence of the attractive species. This reversal of associational resistance we will call "shared doom". A few preliminary investigations failed to find evidence supporting the importance of this phenomenon (Hay 1985, 1986; Pfister and Hay 1988), and to our knowledge, only two cases of shared doom have been noted in the literature. First, Bach (1980) reports that corn is attacked to some degree by cucumber herbivores when grown intermixed with cucumber, whereas normally it is unaffected by these herbivores. Second, Bernstein and Jung (1979) found that fish predation on kelp may increase due to the presence of epibiotic bryozoans on the blades. In our investigation, we used the sea urchin *Arbacia punctulata* to address how epibionts on seaweeds may affect host susceptibility to a generalist consumer.

Sea urchins are important herbivores in many marine habitats, and their effects on plant communities become particularly obvious when urchins are released from predation or switch feeding modes (Harrold and Reed 1985; Elner and Vadas 1990 and literature cited therein). When urchins are abundant, their grazing can determine plant succession, species composition and standing stock of algal communities (Dean et al. 1984; Harrold and Reed 1985; Fletcher 1987; Sousa and Connell 1992; Andrew 1993). The often drastic impact of urchin foraging is not only due to locally very high urchin numbers, but also to the extreme breadth of their diet. For instance, according to Lawrence (1975) and our own observations, the species used in this study, *A. punctulata*, will feed on brown algae, green algae, red algae, foliose and filamentous algae, seagrasses, sponges, hydrozoans, coral polyps, mussels, sand dollars, bryozoans, dead fish, cheese, window screen and wooden clothes pins.

At Radio Island jetty near Beaufort, North Carolina where most plants and animals for this study were collected, omnivorous sparid fishes (*Lagodon rhomboides* and *Diplodus holbrooki*) and urchins (*A. punctulata*) are the most common consumers (Hay 1986; Pfister and Hay 1988). The fishes spend the winter in deeper water offshore and only forage on the jetty from spring to fall. Urchins are present year round, but exhibit strongly reduced foraging activity in winter. During the summer and fall, grazing activity of these omnivores may have a large impact on abundance, species composition and spatial distribution of local algae (Hay 1986; Pfister and Hay 1988).

The goal of this investigation was to evaluate the potential importance of associational resistance and shared doom in affecting urchin feeding preference and the susceptibility of various seaweeds to urchin grazing as a function of associated hosts or epibionts. We addressed the following questions: (1) Does the urchin *A. punctulata* exhibit preferences for certain prey species, or does it feed indiscriminately? (2) Does epibiosis influence grazing by *A. punctulata* on host algae? (3) Can these effects be explained by differential urchin preferences for algal hosts versus epibionts?

Materials and methods

Study area and organisms

Most algae were collected between 0.5 and 2 m below MLW from jetties and pilings around Morehead City and Beaufort (32°42'N, 76°41'W), North Carolina, USA. Only the brown alga *Zonaria tournefortii* was taken 41 km offshore from Wilmington, North Carolina, at a depth of 28 m. Host seaweeds used in this study were the green alga *Codium fragile,* the brown algae *Sargassum filipendula* and *Z. tournefortii* and the red algae *Gigartina acicularis*, *Gracilaria tikvahiae* and *Agardhiella subulata*. Epibiont species found on one or more of these host species in sufficient abundance to be used in this investigation were the brown alga *Ectocarpus* sp. (on *S. filipendula, C. fragile, Gracilaria tikvahiae,* and *Agardhiella subulata*) the red algae *Polysiphonia* sp. (on *S. filipendula, C. fragile, G. acicularis, G. tikvahiae,* and *A. subulata*) and *Audouinella* sp. (on *S. filipendula,* and *C. fragile*), the bryozoans *Bugula neritina* (on *S. filipendula*) and *Membranipora membranacea* (on *Z. tournefortii*), and eggs of the gastropod *Anachis floridana* (on *S. filipendula*). All organisms will be referred to by their generic names in the following text unless first being introduced.

Collections were made between March and May 1993. Algae were placed in a cooler for transport to the lab where they were transferred to a shallow flow-through tank and used in our experiments with live plants within 24 h of collection. Algae designated to be incorporated into artificial food were spun in a salad spinner

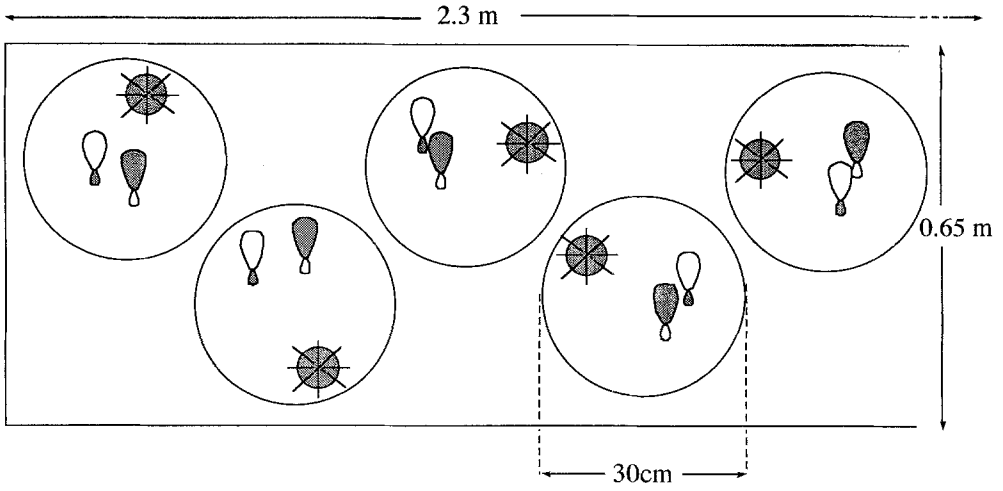

Fig. 1 Set-up of the two-way preference assay. Only half a tank is pictured. One urchin per mesh fence chooses between two alternatives (two live plants or two different plants ground and imbedded in agar), initially positioned at 20 cm from the urchin. Initial movement to a prey and feeding were monitored

to remove excess water, freeze-dried, ground to a fine powder with a coffee grinder and stored at –20°C until used.

All feeding assays were run with the omnivorous sea urchin, *Arbacia punctulata,* which is the only abundant inshore sea urchin and one of the most ecologically important herbivores in this area. Urchins were collected at Radio Island jetty near Beaufort, North Carolina, and kept in shallow flow-through tanks. Between assays, urchins were fed on a variety of available algae, mostly *Gracilaria, Enteromorpha* sp., *Ulva* sp., *Gigartina,* and *Codium.*

Prey choice assays

To determine how epibionts and hosts affected each other's probability of being (a) found and (b) eaten by a generalist grazer, we employed two experimental approaches. First, we tried to determine the position of each host or epibiont on *Arbacia*'s feeding preference hierarchy. Second, we determined whether a host's susceptibility to urchin grazing changed if it was epiphytized. We used whole plants in these assays whenever possible; however, this approach was impossible with small epibionts because they would float free of our experimental containers if they were detached from their host. In these cases, we offered the urchins artificial food made of freeze-dried host or epibiont imbedded in agar. This presentation method incorporates the chemical and nutritional characteristics of the prey, but destroys morphological and certain structural characteristics, some of which could affect urchin feeding. Feeding on hosts versus epibionts was often impossible to quantify rigorously (i.e., mass lost) because we could not get an initial weight on epibionts without removing them from the host. Because we considered this study a "first effort" to look broadly at the question of how epibionts affect host susceptibility to grazers, we were most interested in large and obvious patterns of feeding. Thus, for assays with live plants we did not attempt to carefully quantify amounts eaten, instead we subjectively categorized treatments within each replicate as either heavily consumed (>75% eaten) or not heavily consumed (usually <25% eaten), and measured feeding preferences as the frequency with which a treatment was heavily consumed versus not heavily consumed. Because urchins usually ate most of, or very little of, a food item, this method seemed adequate for documenting the large differences in which we were most interested.

All experiments were run in four 2.3×0.65×0.15 m flow-through tanks. In each tank ten urchins were fenced individually in plastic mesh cylinders (d = 30 cm, h = 20 cm, 1 cm mesh width, see Fig. 1). These 40 urchins were regarded as independent replicates. Urchins were always offered a two-way choice with the two prey items initially being positioned at 20 cm from the urchin and separated from each other by 1 urchin diameter (5–10 cm). Movement to a prey was determined by checking each replicate at about 30 min intervals for the first 8–12 h of the experiment and recording which food was first contacted by the urchin's oral field. Feeding (as opposed to movement to a prey) was measured as the number of replicates in which whole plants of a treatment were heavily consumed (estimated as >75% eaten), or, in the case of the agar-based foods, as the actual amount of food eaten (see below). Because we monitored movement for only 8–12 h, but recorded feeding over longer periods, numbers of urchins recorded feeding on an algal species could exceed numbers recorded moving to that species. On the other hand, choice observations could exceed feeding observations, when single urchins did not feed after having chosen.

Assays with whole plants were conducted within 24 h of plant collection. In most assays, 5 cm-long pieces were cut from the plants and presented to urchins as described above. When plant morphologies were extremely different between species, we tried to visually match plant surface area rather than length. When contrasting clean versus fouled hosts, we used plants that contained no visible epiphytes (= clean) and contrasted these with fouled plants having at least 30% of their surface covered by a given epibiont species. Care was taken to use plant parts of similar age and function (leaves, stipe, with/without reproductive organs, etc.,). Only in the case of *Sargassum* was this not always possible. *Anachis* eggs and *Bugula*, for instance, were found exclusively on older portions of this alga and clean thalli only existed near the younger tips of the plants. While the eggs could be scraped off, this was impossible for the bryozoan. Because a subsequent comparison of clean old versus clean young *Sargassum* parts showed that both were of very similar low preference (contingency table, P = 0.33, n = 19), we assumed that age differences between the plant parts used in this particular assay did not confound the effects of epibionts.

Agar-based foods used in our assays were prepared by incorporating a freeze-dried and powdered organism into agar. For this, 0.72 g of agar were added to 20 ml of distilled water and heated in a microwave until it boiled. The hot agar was then stirred uniformly into 16 ml of cold distilled water containing 2 g dry mass of powdered prey. This mixture was poured into a mold consisting of a rectangular piece of Formica with 2–4 parallel strips cut out. A fiberglass window screen (49 meshes/cm^2) on wax paper was sandwiched between the Formica mold (top) and a PVC sheet (bottom). This 4 layer assemblage was firmly clamped together. The wax paper prevented the artificial food from sticking to the PVC as it solidified. The window screen provided flexible support for the artificial food and permitted a quantification of grazing by counting the numbers of squares from which the urchin had removed the food [see Hay et al. (1994) for an illustration of the molds, methods, and foods produced]. After solidification of the agar, the mold was disassembled, the screen separated from the wax paper and then cut into strips, such that every strip contained two equal-sized squares of the different food types separated by about 2 cm of empty screen. Depending on the amount of pow-

dered organism available, different mold sizes were sometimes used; however, within a given assay, only screens of one size were used. Activity of the urchins (movement and feeding) was monitored every 30 min. To be sure that our results were not compromised by urchins eating all of a preferred food and then eating the less preferred food because no other choice remained, we collected data on the amount of each agar-based food that had been eaten when we first noticed that more than half of either food item had been consumed.

In most of the above experiments, not all of the 40 urchins moved to or consumed a food. In our analyses we used only those replicates where urchins had responded to the prey. In all cases, the actual sample sizes used in our statistical evaluations are presented (Tables 1–5). We used contingency table analyses (or Fisher's exact test, if appropriate due to small cell sizes) to evaluate treatment effects regarding urchins moving to an alga or consuming, versus not consuming, more than 75% of the alga. For the agar-based foods where we could precisely count the number of window-screen squares from which food had been removed, we used a paired *U*-test.

To evaluate the degree to which epibiosis effects on host susceptibility to urchin grazing could result from the relative susceptibility of each host and epibiont to urchin grazing, we used data from the experiments described above to determine *Arbacia*'s relative preference for each prey (i.e., each potential prey was ranked from most to least preferred based on the 28 separate two-way choice experiments described above). Because *Membranipora* sp. could not be separated cleanly from its host (*Zonaria*), its rank could not be directly determined. We tentatively assigned it to a bryozoan rank with *Bugula*, but because of this uncertainty, *Zonaria/Membranipora* results were not used for the correlations of prey ranks and effects of epibiosis on *Arbacia* feeding reported below.

To get a semi-quantitative idea of how much one prey was preferred over another we added the two "preference" determinations (see Tables 1, 2) for movement to the preferred prey and for consumption of that prey and divided by 2. This assumes that attraction to a prey and feeding on the prey are equally important parameters determining the impact of herbivory. This will not be true for all species (Hay et al. 1986), but should provide a reasonable general ranking. These ranks range from 12 (least preferred) to 1 (most preferred). To predict how a host's susceptibility to urchin grazing would change as a function of being fouled, the theoretical change in rank (δR) of a fouled host was computed as $\delta R = Rh-(Re+Rh)/2$ where Rh = the rank of the clean host and Re = the rank of the epiphyte. The inherent assumption that host and epibiont contribute equally to the prey characteristics (cues) perceived by the urchin is probably an over-simplification. We then used Spearman Rank correlations to evaluate the relationship between expected and observed changes in urchin behavior and feeding as a function of epibiosis.

Results

Twenty-eight paired choice experiments were run to assess urchin preference for six host and six epibiont species [Tables 1 and 2, for assays with live plants and ground plants imbedded in agar (= artificial food), respectively]. Results are presented for (1) movement of urchins to the prey and (2) feeding on the prey. In 15 out of 28 cases, preference for one of the prey species was significantly greater than for the other, either with regard to movement to the prey, feeding on the prey, or both.

Although each experiment was conducted with 40 urchins, there was large among-assay variance in how many urchins responded to the various foods. When high to intermediate preference seaweeds such as *Agardhiella*, *Gracilaria*, or *Codium* were paired (see first two lines of Table 1), 83–93% of the urchins moved to one of the foods and 28–60% of the urchins consumed >75% of at least one of the foods. In contrast, when low preference plants like *Sargassum* and *Zonaria* were paired (see bottom line of Table 1), only 25% of the urchins moved to these foods and only 10% consumed >75% of either food.

Urchins were able to selectively move toward preferred foods in these assays. This is illustrated by the strong positive relationship between the choice item they first contacted and the choice item on which they preferentially fed. In those assays with whole plants where we were able to observe for the same urchin individual both "movement to" and "consumption", 90% of the urchins (196 of 218) moved first to their preferred food ($P = 0.0002$, contingency table analysis). In only 10% of the observations did urchins switch prey before starting to feed.

To assess this relationship more thoroughly, we used the data from Table 2 and correlated "preference" (= % of species A – % of species B) regarding movement to a

Table 1 Results of the preference assays using live plants. [+]: *A* and *B* give the numbers of active urchins crawling onto plants of species A or B, respectively. *A%* and *B%* are the corresponding percentage values with 100% being the total number of choices made during the 8–12 h over which the urchins were monitored. [++]: *A* and *B* are the numbers of urchins heavily consuming (i.e.,>75% of the plant consumed) species A or species B, respectively. *A%* and *B%* are the corresponding percentage values with 100% being the number of feeding urchins
*=significant difference ($P<0.05$)

Prey species		"Movement to" [+]						"Consumption" [++]					
Species A	Species B	#		%		Preference (A%–B%)	*P*	#		%		Preference (A%–B%)	*P*
		A	B	A%	B%			A	B	A%	B%		
Agardhiella	*Gracilaria*	22	15	59	41	18	0.1	6	5	55	45	10	0.67
Agardiella	*Codium*	20	13	61	39	22	0.085	18	6	75	25	50	*0.0005
Codium	*Sargassum*	14	6	70	30	40	*0.01	14	0	100	0	100	*0.0001
Codium	*Zonaria*	12	1	92	8	84	*0.0001	18	0	100	0	100	*0.0001
Gigartina	*Codium*	10	10	50	50	0	1	17	3	85	15	70	*0.0001
Gigartina	*Sargassum*	13	6	68	32	36	*0.023	8	2	80	60	0.007	
Gracilaria	*Codium*	17	3	85	15	70	*0.0001						
Gracilaria	*Gigartina*	12	8	60	40	20	0.2						
Zonaria	*Sargassum*	6	4	60	40	20	0.42	3	1	75	25	50	0.16

Table 2 Results of the preference assays using ground prey tissue imbedded in agar. Designations are as in Table 1 except that the actual number of agar squares (±1 SE) eaten was measured in this assay

Prey species		"Movement to" [+]						"Consumption" [++]						
Species A	Species B	#		%		Preference (A%–B%)	*P*	Screeen size	Squares eaten		%		Preference (A%–B%)	*P*
		A	B	A%	B%				A	B	A%	B%		
Agardhiella	*Bugula*	11	5	69	31	38	* 0.034	50	31±6	23±5	57	43	15	0.46
Anachis eggs	*Audouinella*	9	2	82	18	64	* 0.003	50	28±4	13±4	68	32	37	* 0.027
Anachis eggs	*Ectocarpus 2*	8	7	52	48	4	0.71	50	27±5	17±6	61	39	23	0.27
Anachis eggs	*Gracilaria*	5	5	50	50	0	1	50	27±7	22±8	55	45	10	0.69
Audouinella	*Codium*	28	14	67	33	34	* 0.02	210	115±11	32±9	78	22	56	* 0.0001
Audouinella	*Ectocarpus 1*	12	4	75	25	50	* 0.005	50	43±4	7±4	86	14	72	* 0.0001
Audouinella	*Ectocarpus 2*	12	12	50	50	0	1	50	19±5	17±5	53	47	6	0.78
Audouinella	*Polysiphonia*	8	8	50	50	0	1	80	36±7	33±8	52	48	4	0.9
Bugula	*Anachis eggs*	8	6	57	43	14	0.45	50	16±5	26±6	38	62	–24	0.38
Bugula	*Audouinella*	12	5	71	29	42	* 0.016	210	80±18	73±15	52	48	5	0.81
Bugula	*Ectocarpus 1*	11	5	69	31	38	* 0.034	80	60±8	21±8	74	26	48	* 0.024
Bugula	*Polysiphonia*	15	11	58	42	16	0.27	80	48±7	42±7	53	47	7	0.59
Codium	*Ectocarpus 1*	20	16	56	44	12	0.35	210	88±13	64±11	58	42	16	0.22
Ectocarpus 2	*Agardhiella*	13	10	57	43	14	0.38	50	23±5	18±4	56	44	12	0.55
Ectocarpus 2	*Bugula*	14	7	67	33	34	* 0.031	50	23±4	19±4	55	45	10	0.56
Gracilaria	*Ectocarpus 1*	19	4	83	17	66	* 0.001	210	104±14	24±16	81	19	63	* 0.0084
Gracilaria	*Polysiphonia*	7	4	63	37	26	0.2	50	29±8	23±7	56	44	12	0.69
Polysiphonia	*Ectocarpus 1*	9	4	69	31	38	* 0.05	80	61±5	29±7	68	32	36	* 0.002
Sargassum	*Ectocarpus 1*	13	11	54	46	8	0.58	110	45±9	55±9	45	55	–10	0.5

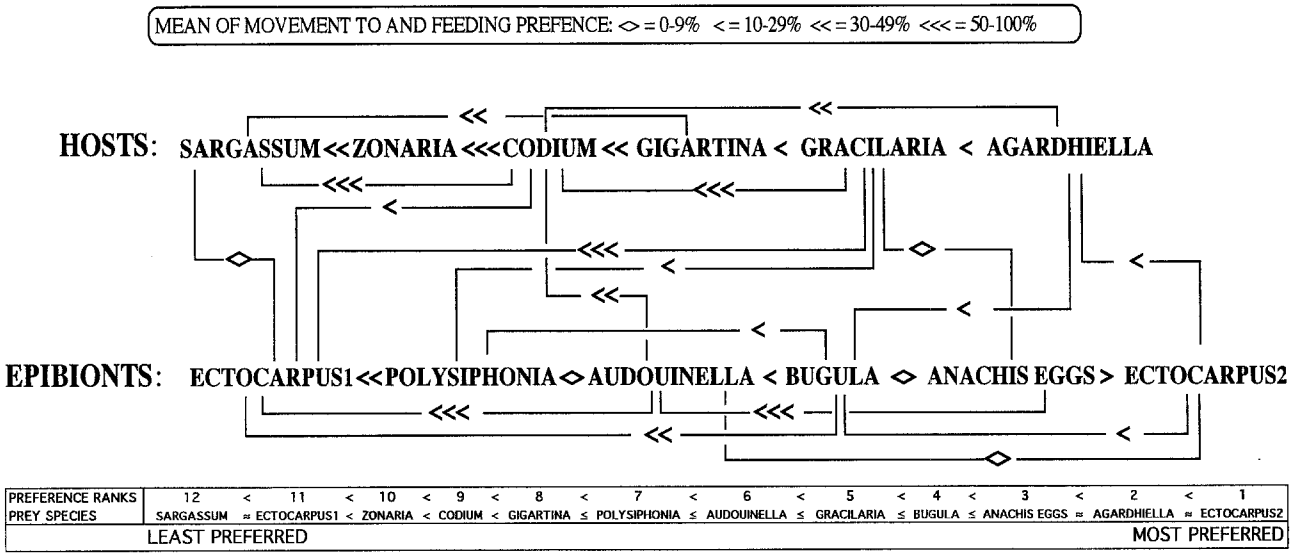

Fig. 2 Ranking of epibionts and hosts by urchin movement to a prey and feeding on that food. Results of the pairwise comparisons are given in Tables 1 and 2, where "preference" is defined as the difference between the percentage of urchins moving to or consuming large amounts of the test species. A key to the meaning of the various symbols is provided at the top of the figure. The final ranking of the 12 species is given at the bottom of the figure. 1 is the most (*Ectocarpus 2*) and 12 the least preferred species (*Ectocarpus 1*), the remaining species were arranged according to direct (A versus B) or indirect comparisons (A versus C and B versus C). Although, species grouped at the extremes of the preference gradient are almost indistinguishable, they were attributed individual ranks based on comparisons with common neighbors. Quantitative data used to construct this preference hierarchy are given in Tables 1 and 2

prey with feeding on that prey. For these 19 assays, there was a strong and significant positive correlation ($r = 0.615$, $P = 0.009$, Spearman rank correlation). Thus, *Arbacia* could sense prey from a distance of 20 cm and selectively move toward preferred prey. A similar correlation run on the whole plant assays (Table 1) produced a similar correlation ($r = 0.625$) but it was not statistically significant ($P = 0.126$). Given the sample size for this correlation was only seven, we suspect that the nonsignificant analysis results from a lack of statistical power rather than the absence of a positive relationship.

In order to understand the effects of epibiosis on host susceptibility to urchin predation and to compare observed and expected results with the models on associational resistance and shared doom, we needed to rank

Table 3 Preference assay for clean hosts versus hosts fouled by various epibionts. "Rank difference" (δR) between clean and fouled host was extrapolated from host (Rh) and epibiont (Re) ranks (see Fig. 2) as δR=Rh–(Rh+Re)/2. At δR<0, the fouled host *B* is expected to be less preferred than the clean host *A*. At δR>0, B should be preferred over A. Urchin movement to a host and feeding on that host are given as numbers of active urchins (choosing and/or feeding). Preference changes are computed as percentage differences of urchins moving to or feeding on fouled versus clean hosts

A Clean host	B Fouled host	Rank Difference	"Movement to"				"Consumption"			
			Urchins Choosing clean host A1	Urchins Choosing fouled host B1	%– Difference	*P*	Urchins eating>75% of clean host A2	Urchins eating>75% of fouled host B2	% Difference	*P*
Gracilaria	*Gracilaria+Ectocarpus 1*	–3	19	10	–48	0.018				
Agardhiella	*Agardhiella+Polysiphonia*	–2.5	9	7	–21	0.48	7	5	–28	0.41
Codium	*Codium+Ectocarpus 1*	–1	15	8	–46	0.039	11	3	–73	0.0012
Gracilaria	*Gracilaria+Polysiphonia*	–1	11	2	–82	0.0004	8	1	–88	0.001
Sargassum	*Sargassum+Ectocarpus 1*	0.5	24	15	–39	0.04	0	0	0	1
Agardhiella	*Agardhiella+Ectocarpus 2*	0.5	5	14	185	0.0035	5	5	0	1
Gigartina	*Gigartina+Polysiphonia*	0.5	11	28	154	0.0001	9	24	167	0.0002
Codium	*Codium+Polysiphonia*	1	4	11	175	0.01	2	4	100	0.24
Codium	*Codium+Audouinella*	1.5	12	28	133	0.0003	9	23	156	0.0005
Sargassum	*Sargassum+Polysiphonia*	2.5	13	26	100	0.0001	0	7	∞	0.0001
Sargassum	*Sargassum+Audouinella*	3	14	23	64	0.036	0	3	∞	0.014
Sargassum	*Sargassum+Bugula*	4	1	17	1600	0.0001	0	3	∞	0.014
Sargassum [b]	*Sargassum+Anachis eggs*	4.5	3	14	367	0.0001	0	19	∞	0.0001
Sargassum [a]	*Sargassum+Anachis eggs*	4.5	1	10	900	0.0001	1	2	100	0.55
Zonaria	*Zonaria+Membranipora*	?	6	17	183	0.0013	3	27	800	0.0001

[a] Originally clean *Sargassum* parts
[b] *Sargassum* parts originally fouled with *Anachis* eggs, then scraped clean

prey species with regard to urchin preference. The 28 pair-wise contrasts of prey susceptibility (Tables 1, 2) allowed us to arrange most prey along an urchin preference hierarchy. For lack of time and material, we could not test all possible 66 pairings. The assumption that A > C when A > B and B > C seems to be justified since we were able to linearly arrange the 12 species (bottom of Fig. 2) without contradiction between significant preference results. However, at both extremes of our proposed urchin preference gradient, distinction between neighbors was not always clear (and there certainly was a problem ranking *Ectocarpus*, the nutritional quality of which seemed to have evolved during the course of these experiments). The ranking in these regions should be viewed with some caution. While most of these ranks are probably valid for this investigation, they should not be regarded as fixed characteristics of the prey species. In the field, shifts might occur as host and epibiont characteristics change with location and season. As one example, *Ectocarpus* was much more preferred at the end of its growing season than 2 months earlier (see Table 2 contrasts of *Audouinella* versus *Ectocarpus* 1 and versus *Ectocarpus* 2 as an example).

The ranking (Fig. 2) and the assays on which it is based illustrate how *Arbacia* consumes a wide variety of species, but selects among these. The urchin exhibits clear preferences, with red algae and animals tending to be preferred over the brown and green algae included in our assays. In initial assays, we also found that urchins selectively ($P < 0.001$) moved to and fed on any of our foods in agar in preference to agar alone.

Comparisons of clean versus fouled host plants indicated that epibionts could dramatically increase or decrease a host's susceptibility to urchin grazing (Table 3). Again, there was a general similarity between patterns of urchin movement toward foods and their willingness to eat those foods when encountered. Although the direction of epibiosis-caused change in movement to prey and feeding on prey was identical in all instances, the amplitude of change differed in a few cases. When low to intermediate preference epiphytes like *Ectocarpus* 1 and *Polysiphonia* (see Fig. 2) occurred on higher preference hosts like *Gracilaria*, these host algae always attracted fewer urchins and were usually fed on significantly less than clean hosts (Table 3). When unpalatable plants like *Sargassum* were fouled by unpalatable species like *Ectocarpus* 1, urchins moved to clean rather than fouled hosts but never consumed large amounts of either food. In contrast, if *Sargassum* was fouled by palatable epibionts, urchins both moved to and fed on the fouled host significantly more than on the clean host (Table 3). As examples, *Sargassum* plants fouled by the filamentous seaweeds *Audouinella* or *Polysiphonia*, the bryozoan *Bugula*, or gastropod eggs were at significantly greater risk of being eaten by urchins than were clean plants ($P < 0.01$, Table 3). In only 1 of 14 cases did epibionts fail to significantly alter the number of urchins moving to a host alga (*Polysiphonia* on *Agardhiella*). Interestingly, a given host (e.g., *Codium, Sargassum*) may experience either increased or decreased susceptibility to urchins due to colonization by different epibionts. Similarly, the same epibiont (e.g., *Polysiphonia*) may cause either increased or decreased host susceptibility, depending on which host alga it colonizes (e.g., *Codium, Gigartina, Gracilaria,* or *Sargassum*, see Table 3).

Table 4 Preference changes caused by epibionts. Positive values: shared doom effects; negative values: associational resistance effects. The predictions are based on the assumption that a fouled host's rank was approximately the mean of epibiont rank and clean host rank, that the most unequal distribution of urchins (100% on one or the other of the two alternatives) should occur when preference between epibiont and host are maximally different, and that an equal distribution of urchins (50% on clean host, 50% on fouled host, 0% difference) should be observed for pairings of equally preferred epibiont and host (see text for details). The percentage values for choice (feeding) are calculated as the percentage of urchins moving to (feeding on) fouled host algae minus the percentage of urchins moving to (feeding on) clean host algae with 100% being the total number of active urchins in a given experiment (raw data in Table 3)

Association (epibiont/host)	Prediction %	Choice %	Feeding %
Anachis eggs/Sargassum	80	64	100
Bryozoa/Sargassum	70	88	100
Bryozoa/Zonaria	60	48	80
Audouinella/Sargassum	50	24	100
Polysiphonia/Sargassum	40	34	100
Audouinella/Codium	30	40	44
Polysiphonia/Codium	20	46	33
Ectocarpus 2/Agardhiella	10	48	0
Polysiphonia/Gigartina	10	44	46
Ectocarpus 1/Sargassum	−10	−24	0
Polysiphonia/Gracilaria	−20	−70	− 78
Ectocarpus 1/Codium	−30	−30	− 58
Polysiphonia/Agardhiella	−50	−16	− 16
Ectocarpus 1/Gracilaria	−70	−32	ND

Whether a change of attractiveness occurs, and whether it is a decrease or increase, seems to depend on the urchins' differential preference for epibiont versus host alga in a given association. A high preference epibiont on a low preference host increased urchin preference for the fouled host relative to its clean conspecifics; a low preference epibiont on a high preference alga usually decreased host susceptibility (Table 3). If we use Fig. 2 and $\delta R = Rh - (Re+Rh)/2$, where Re and Rh are epibiont rank and host rank, respectively, to calculate expected alterations in rank due to epibiosis and correlate this with the observed change in urchin behavior due to epibiosis, we find that changes due to epibiosis are closely correlated to expected differences in rank between clean and fouled host algae ($r = 0.74$, $P = 0.01$ and $r = 0.90$, $P = 0.023$ for changes in urchin movement to hosts and feeding on hosts, respectively).

Predicted changes in urchin behavior based on rank differences between epibiont and host species versus actual results are compared in Table 4, and Figs. 3 and 4. Our prediction was simply that pairing epibiont and host of very different preference ranks would lead to a more drastic change of host susceptibility to urchin predation, than pairing two equally preferred species. Extremely disproportional urchin grazing (± 100%) on clean versus fouled host is expected when a highly preferred host (e.g., *Agardhiella*) is colonized by the least preferred

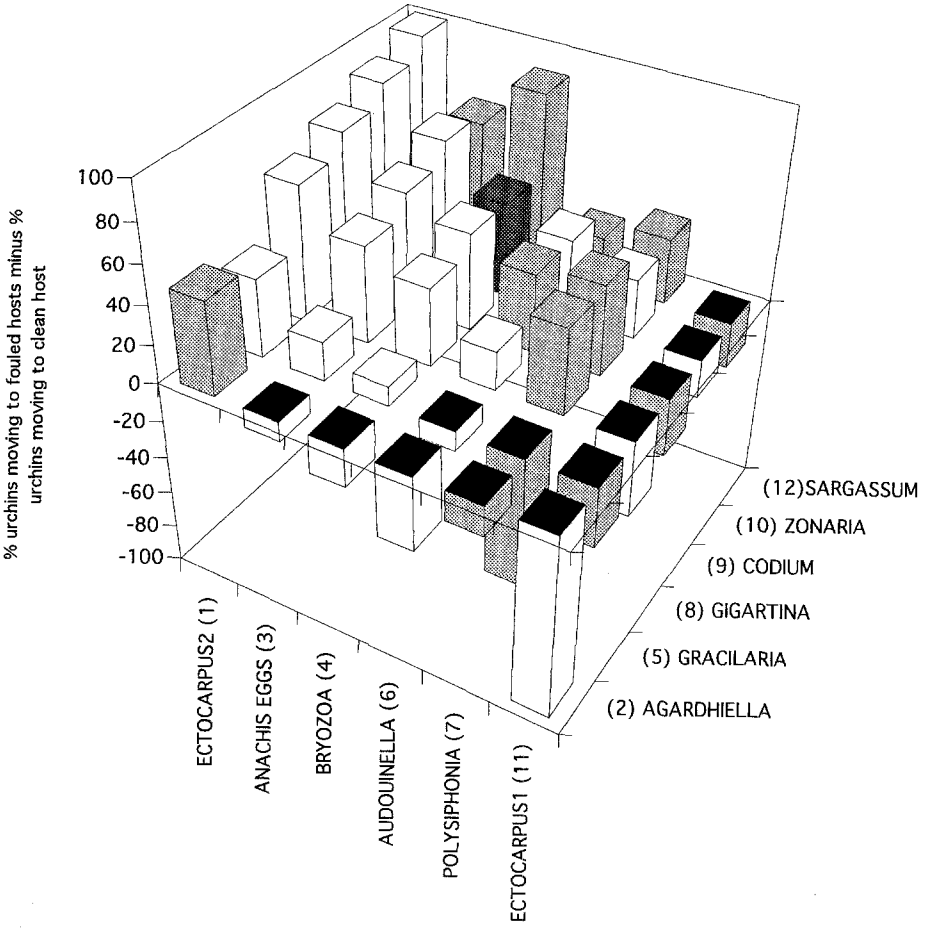

Fig. 3 The predicted (*white columns*) and observed (*shaded columns*) changes in urchin movement to a prey species due to presence of epibionts (data from Table 4). Positive values: shared doom effects; negative values: associational resistance effects. Columns with black bottoms represent negative changes. In this presentation shaded columns (= results) have replaced predicted (white) columns, but the latter's values can be found in Table 4. The *darker shaded column* gives the results for the epibiotic association *Membranipora/Zonaria*. We are somewhat uncertain as to *Membranipora's* position on the urchin preference gradient because we could not adequately separate it from its host and test urchin attraction for it alone. We tentatively assigned it a rank similar to the other bryozoan *Bugula*. Preference ranks for hosts and epibionts are given in parentheses

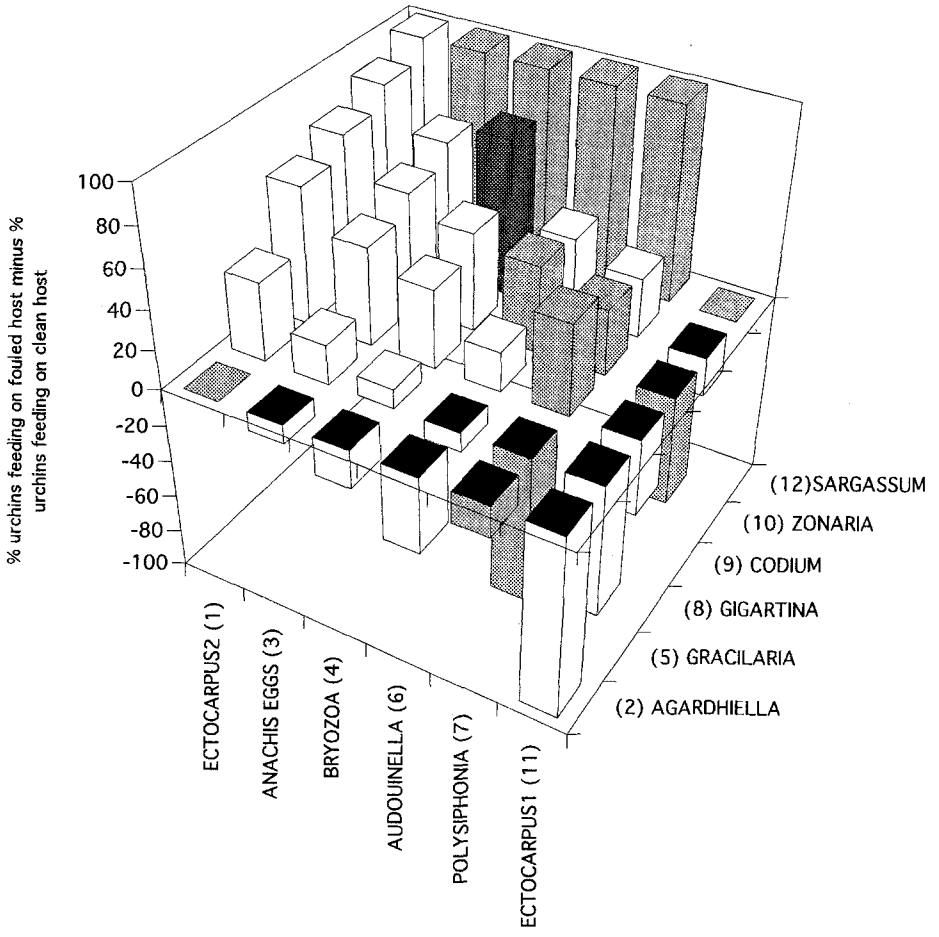

Fig. 4 This graph parallels Fig. 3 and is based on the same experiments, but gives the results of feeding rather than movement to a prey. Positive values: shared doom effects; negative values: associational resistance effects

Table 5 A comparison of urchin movement to lower preference (food *B*) and higher preference (food *A*) hosts when the lower preference host is clean or fouled by more palatable epibionts (ranks in parentheses). Comparing these data with the algal rankings shown in Fig. 2 indicates that palatable epibionts can cause lower preference hosts to rise 3–4 ranks and become indistinguishable from normally higher preference prey

Prey species		"Movement to"			
Species A (rank)	Species B (rank)	Urchins moving to		Significant difference?	
		A	B		*P*
Codium (9)	Sargassum (12)	14	6	Yes	0.01
Codium (9)	Sargassum (12)+Audouinella (6)	9	9	No	1
Codium (9)	Sargassum (12)+Anachis eggs (3)	9	8	No	0.78
Gracilaria (5)	Codium (9)	17	3	Yes	0.0001
Gracilaria (5)	Codium (9)+Audouinella (6)	15	17	No	0.6

epibiont (e.g., *Ectocarpus* 1), or vice versa. The figures show that the results fit the model well ($0.74 < r < 0.9$ with $P < 0.05$), especially where direction of change (increase versus decrease) is concerned. The only exceptions involved *Ectocarpus*, the one species that switched ranks during this investigation.

Urchins occasionally grazed epiphytes without consuming the host. This was usually observed in associations between very low preference hosts and high preference epibionts (e.g., *Sargassum* with *Audouinella, Sargassum* with *Bugula, Sargassum* with *Anachis* eggs, *Zonaria* with *Membranipora*). With regard to the results in this investigation, these cases would register in the "movement to" category (fouled host chosen) but not in the feeding category (fouled *host* not consumed). Even so, this aspect of urchin behavior may have important ecological implications, as discussed later.

The presence of epibionts not only changes the host's attractiveness as compared to clean conspecifics, it can also make the host alga shift ranks and become a prey item equivalent to formerly less or more preferred species (Table 5). Thus, the association *Codium* plus *Audouinella* became as attractive as *Gracilaria* (up four ranks) and *Sargassum* plus *Polysiphonia* or *Sargassum* plus *Anachis* eggs rose to the rank of *Codium* (up three ranks; see Fig. 2 for ranks).

A quite different case of rank change is illustrated by *Ectocarpus*. This epibiont was among the least preferred

of the algae tested when collected in March (*Ectocarpus* 1), yet proved to be highly preferred when collected in the same area during May (*Ectocarpus* 2). We did not identify the thousands of small plants in these large collections of *Ectocarpus* to species, but these collections came from the same general location so we assume that *Ectocarpus* 1 and *Ectocarpus* 2 could have been the same species rather than just related species within the genus. If this is the case, this extreme change in plant quality may be one aspect of the seasonal decline of this genus. *Ectocarpus* disappears from this area in early summer, presumably due to temperature stress, but possibly caused by an alteration in its susceptibility to herbivores.

Discussion

Plant associations can alter herbivore impact on particular species by diverting herbivores to more palatable plants (the attractant/decoy scenario of Atsatt and O'Dowd 1976), by interfering with herbivore ability to locate and recognize palatable plants when they occur among unpalatable species (the associational resistance or repellent plant scenarios of Atsatt and O'Dowd 1976; Hay 1986; Littler et al. 1986; Pfister and Hay 1988), or by lowering relative abundance of herbivores (Tahvanainen and Root 1972; Root 1973; Atsatt and O'Dowd 1976). One of the closest possible associations between different species – epibiosis – is relatively unexplored in this respect.

Effects of epibiosis on herbivore feeding might vary with herbivore size relative to its prey and with the breadth of the herbivore diet. Studies of associational resistance in terrestrial communities have usually focused on herbivory by small, relatively specialized insects (Tahvanainen and Root 1972; Root 1973; Atsatt and O'Dowd 1976; Bach 1980). In contrast, studies of associational resistance in marine systems have focused primarily on larger generalist herbivores like urchins and fishes (Hay 1986; Littler et al. 1986; Pfister and Hay 1988). Given that larger generalists are the major herbivores in marine communities (Hay and Steinberg 1992), this focus is appropriate but the patterns demonstrated in these studies of larger herbivores might not be predictive for smaller mesograzers that view seaweeds as both foods and living sites (Hay et al. 1987; Hay 1992). Feeding and plant choice preferences for these smaller herbivores can be complex in that choices of food quality may be constrained by the habitat quality of the food plant or the epiphytes on that plant (Brawley 1992; Hay 1992; Duffy and Hay 1994). Additionally, although fouled plants often attract greater densities of small grazers such as amphipods, these mesograzers may selectively graze either the epibionts or the host, depending on the species-specific nature of the amphipod feeding preferences (Duffy 1990).

The sea urchin used in our assays consumed a broad variety of seaweeds and animals, and should be considered a generalist omnivore. Although they were very generalized in their feeding, these urchins exhibited clear and consistent preferences that enabled us to rank the prey species, both epibionts and hosts, with regard to urchin preference. In this regard, movement toward a food and feeding on that food gave similar results. The consistency of attraction to preferred foods suggests that urchins search using chemical cues. This observation is consistent with Vadas' (1977) report that chemotactic responses and feeding preferences were correlated for the urchins *Strongylocentrotus droebachiensis* and *S. franciscanus*. In more limited studies with the same species of urchin we used in this investigation (*Arbacia punctulata*), Hay et al. (1986) detected some chemotaxis while Pfister and Hay (1988) could not detect chemotaxis. However, these investigations tested only a limited number of host algae, and effects of epibionts were not considered.

Our study clearly demonstrates that epibiosis can dramatically alter host susceptibility to urchin grazing. Changes may occur in either direction with fouled hosts becoming more preferred or less preferred than clean conspecifics. The direction and degree of change depends on the sign and amount of difference between the ranks of the epibiont and host. A more attractive epibiont increases the attractiveness of the host alga while a less attractive epibiont decreases attractiveness (Table 3). Urchins choosing between clean and fouled algae usually behave as if the preference rank of the epibiont/host association were the mean of the respective ranks of epibiont and clean host (Figs. 3, 4). Fouling of hosts significantly affected movement of urchins in 13 of our 14 assays and significantly affected feeding in 9 of 13 assays (Table 3). Fouling by palatable epibionts had a large enough effect on urchin preferences to make relatively unpalatable hosts indistinguishable from hosts that the urchins much preferred (see Table 5).

This effect of epibiosis on algal susceptibility to herbivory could affect both ecological and evolutionary patterns of plant-herbivore and host-epibiont interactions. Hosts fouled by higher preference epibionts could suffer not only the direct negative effects of being fouled (Davis et al. 1989; Wahl 1989; Williams and Seed 1992) but also may experience increased rates of grazing (Table 3). In contrast, fouling by less preferred epiphytes could increase host fitness if the decrease in herbivore damage was greater than the negative effects of fouling. Epibiotic associations that reduce grazing on the host fit the associational resistance model of Atsatt and O'Dowd (1976). We are aware of only three reports involving host protection by epibionts. Feifarek (1987) described how an epibiotic sponge impedes starfish predation on a spiny oyster, Barkai and McQuaid (1988) found that welks in shells overgrown by a bryozoan were resistant to lobster predation, and Gil-Turnes et al. (1989) found that bacteria growing on the surface of shrimp embryos chemically defended the embryos from pathogenic fungi. While fouling by certain epibionts decreased urchin grazing on some hosts in our assays, it was not clear that this decrease resulted from a repellency produced by the epi-

biont. In preliminary assays where we offered urchins a choice between agar-based foods with various algae versus the agar base alone, urchins always moved to or ate the agar with algae in preference to the agar alone. This suggests that none of the seaweeds we used chemically repelled urchins. In the cases of associational resistance that we documented, attractive exudates of the host must have been diluted or masked by less attractive exudates of the epibiont. This effect amounts to chemical camouflage rather than repellency.

No examples of Atsatt and O'Dowd's (1976) attractant/decoy scenario were observed. An epibiotic association is probably too close spatially for large herbivores like urchins to be detracted from a palatable host by its more palatable epibionts. It should be mentioned in this context that on some rather low preferences hosts (*Sargassum, Zonaria, Codium*) the urchins often scraped off the more palatable epibionts and consumed little of the host. Yet, even in these cases, the grazing of epibionts did not benefit the host because invariably more of the fouled host plants than of the clean hosts were consumed or damaged by the scraping. Indeed, in the field, urchins could be attracted to patches of moderately preferred algae (e.g., *Codium*) by the presence of highly attractive epibionts (e.g., *Audouinella*). After scraping off the epibionts, and with no species of higher preference near, they might then feed on the host.

A reverse effect of epibiosis – shared doom – where close association between different species increases predation on one of the partners has rarely been observed previously. Bach (1980) mentioned how normally immune corn may be moderately attacked by cucumber herbivores when grown intermixed with cucumber, and Bernstein and Jung (1979) describe a case where bryozoans growing on the kelp *Macrocystis pyrifera* increases fish feeding on the kelp blades. In our study, associations between a palatable epibiont and a less palatable host usually produced increased grazing on the fouled host as compared to the clean host, thus enhancing the host's susceptibility to herbivory (Table 3; Fig. 4).

One may argue that the difference between associational resistance and shared doom is merely a matter of perspective and that in both scenarios the association between a high preference organism and a lower preference host increases fitness of the palatable prey, which is the point of reference in most previous studies. This may be true, but it ignores the question of how epibiosis affects the host's susceptibility to herbivores. In this investigation, our point of reference was the host plant, regardless of whether it was the less or the more attractive of the two partners. Furthermore, we show that in very close spatial associations like epibiosis, there is a cost in association with a more palatable prey, something rarely described previously and quite opposite to the attractant/decoy plant model of Atsatt and O'Dowd (1976). We suggest that associations lead to shared doom when the association is spatially too close to allow discriminative grazing (which obviously also depends on consumer size and agility) and when both organisms can be included in the consumer's diet.

Obviously, epibiont mass relative to host mass has a bearing on the amplitude of the preference change due to epibiosis. Epibionts may have to cover a sizable portion of the host in order to influence herbivore preference. A previous study indicated that palatable algae gain protection from fish by living on unpalatable hosts only so long as their biomass remains below about 15% of the host's mass (Hay 1986). The significance of epibiont/host mass ratios may lie in their relative contribution to the optical (fish) and chemical (fish and urchins) search cues used by the consumers. For our interpretation of preference changes due to epibiosis, we arbitrarily attributed the fouled host a rank representing the arithmetic mean between epibiont and clean host, pretending that each partner contributes 50% to the chemical aura sensed by the urchins. This simplification may rarely be true, but the strong and significant correlation between observed patterns and those predicted using this assumption (Figs. 3, 4) suggests that this assumption is, at least, qualitatively reasonable.

It can be argued that the observed differences in urchin preference with regard to clean versus fouled conspecifics might not be a direct effect of the presence of epibionts. Rather, epibiosis and preference change could be due to a common cause, such as a missing antifouling and antifeeding compound in the fouled host. This seems improbable. First because the same host may experience either increased or decreased herbivory depending on the particular epibiont fouling it. It seems unlikely that the lack of one defensive compound could provoke opposite behavioral patterns in the same predator, or that fouling by different epibiont species is due to the absence of different defense compounds which would cause different grazing behavior in *Arbacia*. Second, the most convincing test for the causal role of epibionts in the observed preference changes would have been to compare feeding on fouled hosts with feeding on hosts stripped of their epibionts. Regrettably, in the majority of the associations studied it proved impossible to completely remove epibionts without damaging host tissue. Only *Anachis* eggs could be easily separated from *Sargassum* blades. The feeding difference between fouled and cleaned *Sargassum* was even greater than between fouled and originally clean *Sargassum*. (Table 3). Thus, differences in chemistry between clean and fouled (then cleaned) host were not accountable for the differential grazing behavior of the urchins.

If epibiosis changes herbivore impact, then herbivore pressure, acting on (inducible?) antiherbivore defenses (which can also function as antifouling compounds, see Schmitt et al. in press) or producing differential survival of fouled versus clean hosts, could determine the occurrence and distribution of epibiotic associations in a community. As an example, at the site from which we collected most of our organisms, several palatable algae grow on hard substrata in winter when fish herbivory is low, but are exclusively found as epibionts on unpalatable algae in summer when omnivorous fishes are abundant (Hay 1986). This associational resistance was only

effective for the epibiont as long as its biomass was low relative to that of the host. At higher relative epibiont mass, the palatable epibiont was rapidly consumed. There were, however, no fish-caused negative effects (i.e., shared doom) on the host. In contrast, Bernstein and Jung (1979) reported a log-linear relation between percentage cover of a palatable bryozoan on *Macrocystis pyrifera* blades and feeding rate (number of bites) of fish on the fouled blades. Thus, whether consumers of palatable epibionts clean the host (see Duffy 1990) or subject the host to shared doom probably depends on the size and feeding mode of the consumer relative to the host and epibiont.

The fact that epibionts profoundly affect herbivory adds a new dimension to our understanding of host-epibiont associations. Epibiosis is surprisingly common in the marine environment despite a reasonable assumption that disadvantages for the host will promote the evolution of efficient antifouling defenses. Saving on costly defenses has been cited repeatedly as a possible explanation for why fouling is so common (Davis et al. 1989; Wahl 1989; William and Seed 1992). However, in recent years it has been both argued (Hay and Fenical 1988) and shown that defenses do not have to be expensive (Simms and Rausher 1987; Kearsley and Whitham 1992; Karban 1993). So, if savings due to reduced defense costs are not a generally valid reason for tolerance of epibiosis, then maybe there are more advantages to this association than were previously suspected. Associational resistance to predation could be one of them. Effects considered detrimental to the host, like drag increase, shading or reduced access to nutrients, may be outweighed by epibiont-caused protection from consumers under some conditions. On the other hand, the shared doom aspect of epibiosis may constitute a further incentive to deploy antifouling defenses or to evolve secondary metabolites that function against both consumers and epibionts – at least during times when herbivory is intense.

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References

Andrew NL (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. Ecology 74:292–302

Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. Science 193:24–29

Bach CE (1980) Effects of plant diversity and time of colonization on an herbivore-plant interaction. Oecologia 44:319–326

Barkai A, McQuaid C (1988) Predator-prey role reversal in a marine benthic ecosystem. Science 242:62–64

Bernstein BB, Jung N (1979) Selective pressure and coevolution in a kelp canopy community in Southern California. Ecol Monogr 493:335–355

Brawley SH (1992) Mesoherbivores. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. (Systematics Association, special vol 46). Clarendon Press, Oxford, pp 235–263

Davis AR, Targett NM, McConnell OJ, Young CM (1989) Epibiosis of marine algae and benthic invertebrates: natural products chemistry and other mechanisms inhibiting settlement and overgrowth. In: Scheuer PJ (ed) BioOrganic marine chemistry, vol 3. Springer, Berlin Heidelberg New York, pp 86–114

Dean TA, Schroeter SC, Dixon JD (1984) Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two species of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). Mar Biol 78:301–313

Denno RF, McClure MS (1983) Variable plants and herbivores in natural and managed systems. Academic Press, New York

Duffy JE (1990) Amphipods on seaweeds: partners or pests? Oecologia 83:267–276

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304–1319

Elner RW, Vadas RL (1990) Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. Am Nat 136:108–125

Feifarek BP (1987) Spines and epibionts as antipredator defenses in the thorny oyster *Spondylus americanus* Hermann. J Exp Mar Biol Ecol 105:39–56

Fletcher WJ (1987) Interactions between subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. Ecol Monogr 57:89–109

Gil-Turnes MS, Hay ME, Fenical W (1989) Symbiotic marine bacteria chemically defend crustacean embryos from a pathogenic fungus. Science 246:116–118

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169

Hay ME (1985) Spatial patterns of herbivore impact and their importance in maintaining algal species richness. Proc 5th Int Coral Reef Congr 4:29–34

Hay ME (1986) Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. Am Nat 128:617–641

Hay ME (1992) The role of seaweed chemical defenses in the evolution of feeding specialization and in the mediation of complex interactions. In: Paul VJ (ed) Ecological roles for marine natural roducts. Comstock Press, Ithaca, NY, pp 93–118

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Annu Rev Ecol Syst 19:111–145

Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal J, Berenbaum M (eds) Herbivores: their interaction with secondary plant metabolites, vol II. Evolutionary and ecological processes. Academic Press, New York, pp 371–413

Hay ME, Lee RR, Guieb RA, Bennett MM (1986) Food preference and chemotaxis in the sea urchin *Arbacia punctulata*. J. Exp Mar Biol Ecol 96:147–153

Hay ME, Duffy JE, Pfister CA, Fenical W (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68:1567–1580

Hay ME, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. Ecology 75:1714–1726

Karban R (1993) Costs and benefits of induced resistance and plant density for a native shrub, *Gossypium thurberi*. Ecology 741:9–19

Kearsley MJC, Whitham TG (1992) Guns and butter: a no-cost defense against predation for *Chrysomela confluens*. Oecologia 92:556–562

Lawrence JM (1975) On the relation between marine plants and sea urchins. Oceanogr Mar Biol Annu Rev 13:213–286

Littler MM, Taylor PR, Littler DS (1986) Plant defense associations in the marine environment. Coral Reefs 5:63–71

McNaughton SJ (1978) Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. Science 199:806–807

Martin TE (1988) On the advantage of being different: nest predation and the coexistance of bird species. Proc Natl Acad Sci 85:2196–2199

Morris WF, Karieva PM (1991) How insect herbivores find suitable host plants: the interplay between random and non-ran-

dom movement. In: Bernays EA (ed) Insect-plant interactions. CRC Press, Baton Rouge, pp 175–208

Pfister CA, Hay ME (1988) Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. Oecologia 77:118–129

Renaud PE, Hay ME, Schmitt TM (1990) Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. Oecologia 82:217–226

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 431:95–120

Schmitt TM, Hay ME, Lindquist N (in press) Constraints on chemically mediated coevolution: multiple functions for seaweed secondary metabolites. Ecology

Simms EL, Rausher MD (1987) Costs and benefits of plant resistance to herbivory. Am Nat 130:570–581

Sousa WP, Connell JH (1992) Grazing and succession in marine algae. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. (Systematics Association, special vol 46) Clarendon Press, Oxford, pp 425–441

Tahvanainen JO, Root RB (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta crucifera* (Coleoptera: Chrysomelidae). Oecologia 10:321–346

Vadas RL (1977) Preferential feeding: an optimization strategy in sea urchins. Ecol Monogr 47:337–371

Wahl M (1989) Marine epibiosis. I. Fouling and antifouling: some basic aspects. Mar Ecol Progr Ser 58:175–189

Williams GA, Seed R (1992) Interactions between macrofaunal epiphytes and their host algae. In: John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. (Systematic Association, special vol 46) Clarendon Press, Oxford, pp 189–211